NOBANIS –Invasive Alien Species Fact Sheet

Phytophthora ramorum

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Species description

Scientific names: *Phytophthora ramorum* Werres, De Cock & Man in`t Veld, Oomycetes, Chromalveolata.
Synonyms: None.
Common names: Twig and leaf blight (EU), Ramorum leaf blight (North America), Sudden Oak Death= SOD (North America), tamme-äkksurm (EE), maladie de l’encre des chênes rouges (FR), mort subite du chêne (FR), tammen äkkikuolema (FI), europæisk visneskimmel (DK, European isolates) / californisk visneskimmel (DK, North American isolates), Plötslig ekdöd (SE), Plötzliches eichensterben (DE), Nagła śmierć dębu (POL).

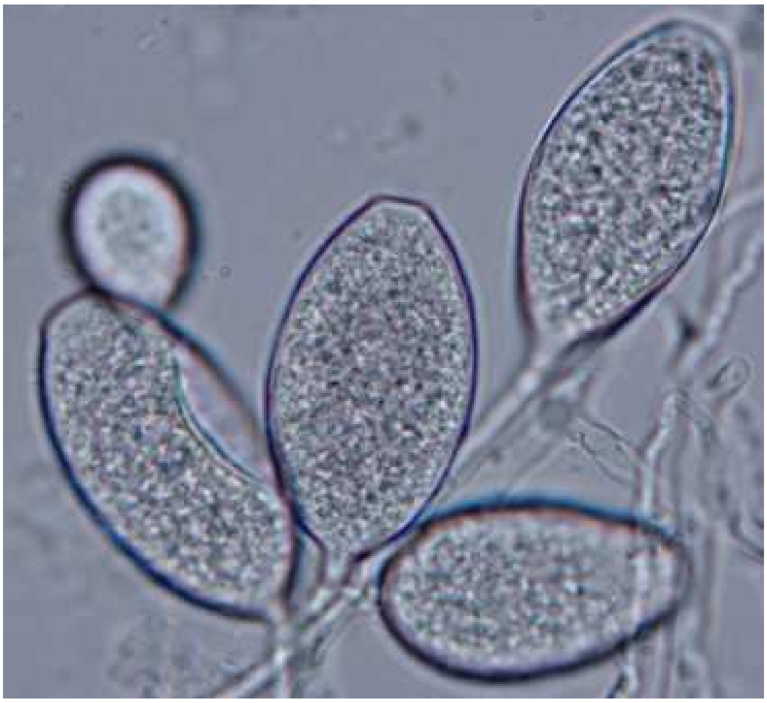

Fig 1. Sporangia of *Phytophthora ramorum* in soil extract water, photo by Arja Lilja.

Fig 2. Branched dendroid-like hyphae of *Phytophthora ramorum* on the bottom of an agar plate, photo by Arja Lilja.

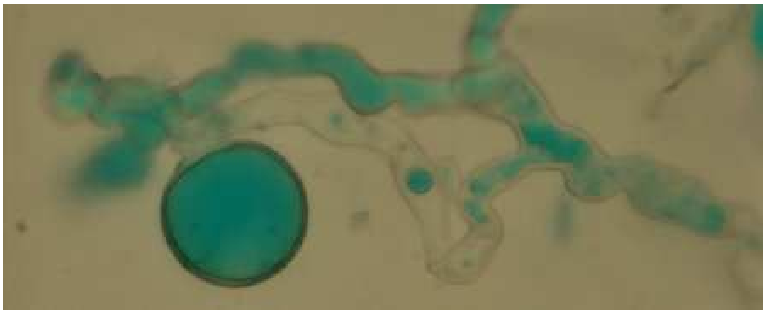

Fig 3. Clamydospore of *Phytophthora ramorum*, photo by Arja Lilja.

Species identification

Phytophthora ramorum is a heterothallic species characterized by abundant production of chlamydospores and elongate, ellipsoid, deciduous sporangia. The mean sporangium length was 43.6 µm ± 5.3 with a range from 20-79 µm, and the mean sporangium width 23.9 µm ± 2.6 with a range from 12-40 µm in measurements done by Werres and Kaminski (2005). Oogonia with amphigynous antheridia were produced by parings with *P. cryptogea* Pethybr. & Laff and other heterothallic *Phytophthora* species representing opposite mating types A1 or A2 (Werres *et al.* 2001, Werres and Kaminski 2005).

There are four clonal lineages of *P. ramorum*; EU1 and EU2 in Europe, as well as NA and NA2 in North America. Before 2012, all isolates found in Europe belonged to one lineage (EU1) and represented predominantly A1 mating type. However, seven isolates have been identified in 2012 to represent a new lineage, EU2. These isolates originated from Northern Ireland and western Scotland, from Japanese larch in addition to three other host plants (Van Poucke *et al.* 2012). Also three isolates of A2 mating type in EU1 lineage have been identified (Werres and De Merlier 2003, Vercauteren *et al.* 2011a).

In North America, NA1 is responsible for sudden oak death and is the most common lineage in US nurseries (Goss *et al.* 2009a, b). Isolates belonging to the NA2 genotype have also been found in some US nurseries, but it is the most common lineage in Canadian ornamentals (Goss *et al.* 2011). Most North American isolates represent A2 mating type, but a few isolates of *P. ramorum* of the A1 type have been reported from horticultural nurseries (Hansen *et al.* 2003).

The EU phytosanitary legislation (Commission Decision 2002/757/EC) concerning plant import distinguishes between European and non-European isolates of *P. ramorum*.

Native range

Phytophthora ramorum has most likely been separately introduced into North America and into Europe (Rizzo *et al.* 2005). *P. ramorum* is phylogenetically closely related to and shows various common features with *P. lateralis* Tucker & Milbrath, and thus these species are likely to share a common region of origin. Recent findings of *P. lateralis* in an old-growth forest of *Chamaecyparis* in Taiwan (Webber *et al.* 2012, Brasier *et al.* 2010) suggest that the geographic origin of *P. ramorum* is also likely to be East Asia.

Alien distribution

History of introduction and geographical spread

In 2001, a new *Phytophthora* associated with a twig blight disease on *Rhododendron* and *Viburnum* in Germany and Netherlands was described as a new species, *P. ramorum* (Werres *et al.* 2001). Later it was found to be responsible for the Sudden Oak Death disease (SOD) of *Quercus* and *Notholithocarpus* spp. in California, USA (Rizzo *et al.* 2002, Kliejunas 2010). The spread of *P. ramorum* in North America has been very rapid. The disease was first discovered on *Notholithocarpus* spp. near Mill Valley in 1995, and since then it has spread throughout the coastal counties around the San Franscisco Bay area where most of *N. densiflorus* (Hook. & Arn.) Manos, Cannon & S.H.Oh, *Q. agrifolia* Née, and *Q. kelloggii* Newberry trees have died (Rizzo *et al.* 2002, Davidson *et al.* 2002, 2005). The disease is currently present also in Oregon and Southwestern Canada (Davidson *et al.* 2005, Hansen *et al.* 2008, Kliejunas 2010).

P. ramorum has been found mainly in nurseries and garden centres in many European countries, *e.g.* in Belgium, Croatia, Czech Republic, Denmark, Finland, France, Germany, Greece, Ireland, Italy, Lithuania, Norway, Poland, Serbia, Slovenia, Spain, Sweden, Switzerland and the UK (Werres *et al.* 2001, Delatour *et al.* 2002, Moralejo and Werres 2002, Orlikowski and Szkuta 2002, De Merlier *et al.* 2003, Heiniger *et al.* 2004, Orlikowski *et al.* 2004, Pintos *et al.* 2004, Zerjav *et al.* 2004, Orlikowski 2005, Swedish Board of Agriculture 2011, Herrero *et al.* 2006, Husson *et al.* 2007, Bulajić *et al.* 2010, Lilja *et al*. 2007, EPPO 2011, Tsopelas *et al.* 2011). In Estonia *P. ramorum* has been found repeatedly since 2006 during border control but it has never been found in nature or in nurseries (Agricultural Board of Estonia, 2010). In the UK and Norway, also wild bilberry samples, collected from heathland and a semimanaged park, respectively, have been found positive for *P. ramorum* (DEFRA 2010, Herrero *et al.* 2011).

In the UK and the Netherlands *P. ramorum* has also been found on mature trees (Brasier *et al*. 2004, Anonymous 2004), but before 2009, always in the proximity of *Rhododendrons*. In 2009, *P. ramorum* was reported for the first time from a semi-natural environment and a conifer species causing widespread dieback and mortality of *Larix kaempferi* (Lam.) Carr. (Japanese larch) in southwest England. It was subsequently detected on the same tree species in Wales, Northern Ireland and the Republic of Ireland (Brasier and Webber 2010). It has also been found on *Larix decidua* P. Mill. (European larch). Before the disease epidemic on larch, *P. ramorum* had been considered more or less harmless to conifer species. The pathogen represents predominantly the EU1 lineage, so the recent "Sudden Larch Death" is probably the result of a host jump, and not an introduction of a new *P. ramorum* genotype. The new lineage EU2 from Northern Ireland and western Scotland (from Japanese larch plus three other host plants) however, probably represents a second and more recent introduction to Europe than EU1 (Van Poucke *et al*. 2012).

Pathways of introduction

It is believed that *P. ramorum* has entered western North America and Western Europe in the late twentieth century, and imported, infected ornamentals have been the main introduction pathway. The mating type and lineage distribution suggest more than one separate introduction into Europe and into North America from a third location (Ivors *et al.* 2006, Prospero *et al.* 2007, Mascheretti *et al.* 2008, Goss *et al.* 2011, Grünwald *et al.* 2012). Migration from Europe to North America has been shown to be more likely than bidirectional migration (Goss *et al.* 2011).

Alien status in region

In Europe, *P. ramorum* was first found on *Rhododendron* and *Viburnum*, but later it has been isolated on a variety of plant genera and species, *e.g. Arbutus*, *Calluna vulgaris* (L.) Hull, *Camellia, Hamamelis, Kalmia, Laurus, Leucothoe, Parrotia, Photinia* x *fraseri, Pieris, Syringa, Vaccinium myrtillus* L. and *V. vitis-idaea* L., (Orlikowski and Szkuta 2002, Werres and De Merlier 2003, Beales *et al.* 2004a, Beales *et al.* 2004b, Husson *et al.* 2007, Herrero *et al.* 2011). In 2003, the pathogen was found on *Quercus falcata* Michx. in the UK, and afterwards on e.g. *Fagus sylvatica* L., *Fraxinus excelsior* L., *Quercus ilex* L., *Q. cerris* L., *Q. rubra* L., *Castanea sativa* Mill., *Taxus baccata* L., *Nothofagus* and *Aesculus hippocastanum* L. (Brasier *et al.* 2004, Lane *et al.* 2004, Anonymous 2004, Orlikowski *et al.* 2004, Orlikowski 2005, Sansford *et al.* 2010, DEFRA 2010). In 2009 the first conifer genus, *Larix*, was added to the host list following the extensive epidemic on Japanese larch in the UK (Brasier and Webber 2010).

In North America, tree hosts are besides *N. densiflorus*, *Q. agrifolia*, *Q. kellogii* and *Q. wislizeni* A.DC., species such as *Q. chrysolepis* Liebm., *Umbellularia californica* (Hook. & Arn.) Nutt., *Sequoia sempervirens* (D. Don) Endl., *Pseudotsuga menziesii* (Mirb.) Franco, *Abies grandis* (Douglas ex D. Don) Lindley, *Acer macrophyllum* Pursh and *Aesculus californica* (Spach) Nutt. The pathogen has also been found on *Arbutus menziesii* Pursh, *Arctostaphylos manzanita* Parry, *Camellia* spp., *Corylus cornuta* Marsh., *Heteromeles arbutifolia* (Lindl.) M.Roem., *Lonicera hispidula* (Lindl.) Dougl. ex Torr. & Gray, *Loropetalum chinense*, *Maianthemum racemosum* (L.) Link, *Pittosporum undulatum* Vent., *Rhamnus californica* Eschsch., *Rhododendron* spp., *Rosa gymnocarpa* Nutt., *Rubus spectabilis* Pursh, *Toxicodendron diversilobum* (Torr. & A.Gray) Greene, *Rhamnus purshiana* DC., *Trientalis latifolia* Hook. and *Vaccinium ovatum* Pursh. (Davidson *et al.* 2002, Goheen *et al.* 2002, Rizzo *et al.* 2002, Knight 2002, Hong 2003, Hüberli *et al.* 2004, 2005, Murphy and Rizzo 2003, Hansen *et al*. 2005, Maloney *et al.* 2005, Vettraino *et al.* 2006, Blomquist *et al.* 2012, USDA 2012).

Today over 40 genera have been susceptible to this pathogen in inoculation trials (Denmann *et al.*

2005, Hansen *et al.* 2005, Tooley and Kyde 2007, Moralejo *et al.* 2009). Among the tested plants a few tree species have had very low disease incidence: *Populus tremuloides* Michx., *P. trichocarpa x P. deltoides*, *Pinus contorta* Douglas, *P. ponderosa* Douglas ex C.Lawson, *P. nigra* var. *maritima*, *P. sylvestris* L., *Salix hookeriana* Barratt ex Hook. and *S. lucida* Muhl. (Denmann *et al.* 2005, Hansen *et al.* 2005). In an inoculation experiment with Iberian tree species, only *P. pinaster* Aiton, *P. nigra* J.F.Arnold and *P. sylvestris* were ranked from resistant to slightly susceptible according to lesion size (Moralejo *et al.* 2009). Highly susceptible broad-leaved potential host species identified by inoculation tests include *Cornus nuttallii* Audubon, *Prunus emarginata* (Dougl. ex Hook.) Eaton, *Quercus alba* L., *Q. canariensis* Willd., *Q. prinus* L., *Q. pubescen* Willd., *Q. pyrenaica* L., *Q. faginea* Lam., *Q. suber* L. and *Ulmus procera* Salisb. (Denman *et al.* 2005, Hansen *et al.* 2005, Tooley and Kyde 2007, Moralejo *et al.* 2009). *Acer monspessulanum* L., *A. pseudoplatanus* L., *A. saccharum* Marsh., *Alnus glutinosa* L., *A. rubra* Bong., *Betula pendula* Roth., *Carpinus betulus* L., *Corylus avellana* L., *Ilex aquifolium* L., *Juglans nigra* L., *Prunus avium* (L.)L., *Tilia cordata* Mill., *Q. agrifolia, Q. laurifolia* Michx., *Q. nigra* L., *Q. pagoda* Rafin., *Q. phellos* L., *Q. petraea* (Matt.) Liebl., *Q. robur* L., *Q. rubra* and *Q. virginiana* Mill. were also possible hosts, but less susceptible (Denman *et al.* 2005, Hansen *et al.* 2005, Tooley and Kyde 2007). Among conifers *Abies procera* Rehd., *Pinus halepensis* Mill. and *P. pinea* L., have been severely affected by inoculation with *P. ramorum*, and *Picea abies* (L.) H.Karst, *P. sitchensis* (Bong.) Carr., *Sequoia sempervirens* and *Tsuga heterophylla* (Raf.) Sarg. have also been shown to be susceptible, while *Chamaecyparis lawsoniana* (A. Murray) Parl., *Quercus ilex* and *Taxus baccata* have shown only moderate susceptibility (Denmann *et al.* 2005, Hansen *et al.* 2005, Moralejo *et al.* 2009). Jinek *et al.* (2010) tested eastern Canadian forest tree species, and susceptible hosts included *Fraxinus Americana* L., *Betula alleghaniensis* Britt. and *Abies balsamea* (L.) Mill. Many understory species have also been highly susceptible, e. g. *Vaccinium membranaceum* Douglas ex Torr. and *V. parvifolium* Sm. (Hansen *et al.* 2005). Also some container weed species have been shown to be hosts (Shishkoff 2012). *Phytophthora ramorum* is not yet found in Australia, but 21 native Australian plant species have been shown to be moderately or highly susceptible, and several potential sporulation hosts have been identified (Ireland *et al.* 2012).

P. ramorum has been found in many European countries. See table 1 for *P. ramorum* status in the NOBANIS region.

Country	**Not found**	**Not established**	**Rare**	**Local**	**Common**	**Very common**	**Not known**
Austria							X
Belgium					X		
Czech republic		X					
Denmark					X		
Estonia		X					
European part of Russia							X
Finland		X					
Faroe Islands							X
Germany					X		
Greenland							X
Iceland	X						
Ireland				X			
Latvia		X					
Lithuania		X					

Netherlands				X
Norway			X	
Poland		X		
Slovakia	X			
Sweden		X		

Table 1. The frequency and establishment of *Phytophthora ramorum*, please refer also to the information provided for this species at www.nobanis.org/search.asp. Legend for this table: **Not found** –The species is not found in the country; **Not established** - The species has not formed self-reproducing populations (but is found as a casual or incidental species); **Rare** - Few sites where it is found in the country; **Local** - Locally abundant, many individuals in some areas of the country; **Common** - Many sites in the country; **Very common** - Many sites and many individuals; **Not known** – No information was available.

Ecology

Habitat description

The microbe is regarded as a cool-temperate organism with an optimum temperature for growth at 20°C and minimum and maximum at 2°C and 30°C respectively (Werres *et al.* 2001). In the study by Tooley *et al.* (2008), the lower threshold for its 7-day survival in *Rhododendron* tissue was between 10°C and 20°C, and the higher threshold for chlamydospore survival in moistened sand between 35°C and 40°C. In woody plant material, one week of heat treatment at 55 °C was needed to kill the pathogen (Garbelotto 2004). Wet conditions are needed for sporangia production and successful infection. The pathogen has been found in forests, forest and ornamental nurseries, gardens and parks. At the moment, the habitats affected by the most large-scale *P. ramorum* epidemics are the coastal evergreen oak forests in California and *Larix* plantation forests in Great Britain. In England and Wales, it has been shown that county incidence of *P. ramorum* in semi-natural environments increased with increasing precipitation and with declining latitude (Chadfield and Pautasso 2006). CLIMEX models based on studies on the epidemiological variables have been used to create potential distribution maps for P. ramorum establishment in the USA (Venette and Cohen 2006). In Europe, western coastal areas are under the highest risk of *P. ramorum* epidemics (RAPRA 2009).

Reproduction and life cycle

Two types of asexual spores, zoospores (released from sporangia) and chlamydospores, are produced under wet conditions and moderate temperature on infected leaves or twigs. The motile (swimming) zoospores are released from sporangia after landing on susceptible host. They encyst, germinate and penetrate the host tissue, and are thus responsible for new infections. Chlamydospores are the resting structures involved in survival. Under suitable conditions they germinate to produce new hyphae, and in suitable environments, rapid repetition of this asexual cycle can result in epidemics. *P. ramorum* is a heterothallic species and paring of opposite mating types is needed for sexual reproduction. However, sexual structures, oogonia, antheridia and oospores, have not yet been found in nature. In artificial pairings oospores have been produced (Werres and Zielke 2003, Brasier and Kirk 2004), and later also progenies have been obtained in laboratory conditions (Boutet *et al*. 2010). However, the progenies have been shown to contain phenotypic variation and instability in DNA content due to genotypic rearrangements (Vercauteren *et al*. 2012b).

Dispersal and spread

P. ramorum differs from the majority of other *Phytophthora* species in being adapted to an aerial lifestyle. The sporangia of the pathogen are caducous, which means that they are detached from the hyphae and transported locally by rain water splashes. Inoculum is transported up in the canopy and further longer distances by turbulent wind and wind driven rain (Hansen *et al.* 2008). In the case of Sudden Oak Death in the US, foliar infections on woody shrubs or other hosts in the understory have been shown to enable the build-up of an enormous inoculum and subsequent efficient spread to oak stems and thus sustain the epidemic (Rizzo *et al.* 2005). Soil from vehicle tires has been shown to contain viable spores of *P. ramorum*. In addition, hikers have been shown to carry spores on their shoes after visits in infested areas during the rainy season (Tjosvold *et al.* 2002). In the case of the epidemic on *Larix* spp., a new disease dynamic has been observed. In "Sudden Larch Death", the epidemic is not sustained primarily by understory plants like in California; instead *P. ramorum* sporulates efficiently on larch needles high in the tree canopy (Webber *et al.* 2010).

P. ramorum is found relatively often in nurseries, and is thus likely to spread to new locations within a country by infected planting material. It can also spread further into surrounding environment from gardens and parks, which has happened in California, and is suspected for example in the case of bilberry infection in Norway (Herrero *et al.* 2011). In the US, population genetic analysis have revealed migration pathways, that are in agreement with trace forward analyses based on plant shipment routes (Goss *et al.* 2009b). It was also inferred that only a few genotypes are responsible for initiating the infestations across the country. Bark beetles and ambrosia beetles are commonly found on diseased trees but their potential role as vectors has not been studied yet (McPherson *et al.* 2005). Long-range spread of the pathogen appears to be linked to favourable weather patterns (El Nino in California, Filipe *et al.* 2012) and new introduction events (Kliejunas *et al.* 2010). New introduction events between countries primarily occur via international plant trade (Moralejo and Werres 2002, Brasier 2008, Hansen 2007, Santini *et al*. 2012).

Although *P. ramorum* infects the above-ground parts of host plants, it has been also found in the roots of symptomless commercial nursery plants (Vercauteren *et al.* 2013). *P. ramorum* was also experimentally shown to persist in symptomless *Rhododendron* root balls for at least 8 months and in rootless substrates at least 33 months (Vercauteren *et al.* 2013). This symptomless presence in root balls and potting media can contribute to latent spread of this pathogen between nurseries.

Impact

Affected habitats and indigenous organism

Phytophthora ramorum affects the aerial parts of plants and disease symptoms are diverse depending on the plant species. On woody shrubs or small trees such as *Rhamnus* and many other understory hosts such as *Rhododendron*, *P. ramorum* mainly causes leaf lesions or/and twig blight. On *Camellia*, *Griselinia*, *Kalmia*, *Laurus*, *Leucothoe*, *Photinia* and *Syringa* the pathogen causes brown to black leaf lesions (Orlikowski and Szuta 2004, Vettraino *et al*. 2006, DEFRA 2010, Forestry Commission 2013). On *Calluna* apical shoot parts turned brown and infected shoots might have shepherd crook shape (Orlikowski and Szuta 2004). In larger trees, bark infections cause cankers with tarry or rusty colored exudations. The leaves of infected trees may turn brown over a short period, but death may take one or more years (Garbelotto *et al.* 2001). On *Notholithocarpus densiflorus*, the pathogen affects both bark and leaves and death can be rapid. On *Viburnum*, the stem base infection cause wilting and death.

On *Larix* spp., symptoms include black or purple discoloured needles, aborted bud flush, wilting and senescence of dwarf shoots and needle loss. Trees can also often have copious resin bleeding on the trunk, branches and side shoots, in addition to dieback of branches and sometimes of the entire crown. Deep pink to brown phloem lesions are often present under resinous outer bark (Webber *et al.* 2010).

The impact of *P. ramorum* differs depending on the ecosystem and host. In susceptible natural and semi-natural forests, extensive mortality of trees and shrubs can have severe short- and long-term ecological consequences, including significant changes in the structure and composition of the plant and animal communities, as well as increased water run-off and associated soil erosion.

Genetic effects

No genetic effects.

Human health effects

No human health effects have been reported.

Economic and societal effects (positive/negative)

The economic and social impacts of *P. ramorum* have been considerable especially in the US (Kovacks *et al.* 2011) and more recently in the UK. The significant economic impact upon these forest ecosystems results from costs of monitoring and eradication measures, as well as reductions in recreational, cultural, or commodity value. In the US, the most large-scale environmental impact of *P. ramorum* has occurred with the Sudden Oak Death in the coastal woodlands of California and southwestern Oregon. In the UK, the disease has been found mostly on larch trees at over 140 sites and over 4 million trees have been felled. In Ireland, *P. ramorum* has been found in 11 forest sites in 2010. Many noble fir (*Abies procera*), beech (*Fagus sylvatica*) and Spanish chestnut (*Castanea sativa*) trees as well as a single sitka spruce (*Picea sitchensis*) growing in the proximity to the infected larch have also been found to be infected in Ireland (Dept. of Agriculture, Food and the Marine 2011). In nurseries, the economic impacts of *P. ramorum* include losses due to quarantine restrictions and mandatory destruction of infested ornamentals, as well as trade losses.

Many produced plant species in the ornamental nursery industry are known as hosts for *P. ramorum*, and many ecologically and environmentally important woody species have also been hosts or highly susceptible in inoculations. Thus, with the growing international plant trade, more introductions of *P. ramorum* genotypes continue to increase the probability of new outbreaks and epidemics in Europe.

Management approaches

Prevention methods

The spread of *P. ramorum* and its new genotypes into new geographical areas by plant trade should be avoided. The European Commission Decision 2004/426/EC imposes strict import regulations for the host plants of *P. ramorum*. However, the regulation protocols do not completely guarantee prevention of introduction (Brasier 2008), and thus new approaches for regulation are needed.

Eradication, control and monitoring efforts

Management of *P. ramorum* in nurseries through IPM (intergrated pest management) practices include cultural practices, fungicides, and host resistance (Orlikowski 2004, James *et al.* 2012). According to the EU Commission Regulation 2004/426/EC, the national plant protection services are required to sample plants with suspected infections of *P. ramorum* and destroy infected plants together with all other host plants within a 2 m radius. Trade from infected nurseries is suspended and further inspections are required before trade can resume.

Extensive surveys to screen for the presence of *P. ramorum* have been done both in Europe and North America (Forestry Commission 2013, USDA 2012).

Information and awareness

Information to nurseries, environmental managers and the general public on the environmental effects and management of *P. ramorum* is spread by the National Plant Protection Service in each country through information on the Internet.

Knowledge and research

None reported.

Recommendations or comments from experts and local communities

None reported.

References and other resources

Contact persons

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Links

A project within the EU 6th Framework R & D Programme, priority 8.1.B.1. Sustainable management of Europe's natural resources. RAPRA. Risk analysis for *Phytophthora ramorum.*

Bundeanstalt für Land und Forstwirtschaft (BBA). *Phytophthora ramorum*.

Forestry Commission. *Phytophthora ramorum.*

Deparment for Environment Food and Rural Affairs (DEFRA). A threat to our woodlands, heathlands and historic gardens, *Phytophthora ramorum.*

European and Mediterranean Plant Protection Organisation (EPPO). *Phytophthora ramorum.*

Invasive Species Specialist Group (ISSG). *Phytophthora ramorum.*

Swedish Board of Agriculture. *Phytophthora ramorum* angriper rhododendron och många andra arter.

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